A suspension feeding anomalocarid from the early Cambrian

Jakob Vinther[1], Martin Stein[2], Nicholas R. Longrich[3] & David A. T. Harper[4]

[1]Schools of Earth Sciences and Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, United Kingdom. [2]Natural History Museum of Denmark, Copenhagen University, Universitetsparken 15, 2100 Copenhagen Ø, Denmark. [3]Department of Biology and Biochemistry, University of Bath, Bath BA2 7AY, United Kingdom. [4]Palaeoecosystems Group, Department of Earth Sciences, Durham University, Durham DH1 3LE, United Kingdom.

Large, actively swimming suspension feeders evolved several times in Earth's history, arising independently from groups as diverse as sharks, rays, stem teleost fishes[1], and in mysticete whales[2]. Animals occupying this niche have not, however, been identified from the early Palaeozoic. Anomalocarids, a group of stem arthropods that were the largest nektonic animals of the Cambrian and Ordovician, are generally thought to have been apex predators[3-5]. Here we describe new material of *Tamisiocaris borealis*[6], an anomalocarid from the early Cambrian (Series 2) Sirius Passet Fauna of North Greenland, and propose that its frontal appendage is specialized for suspension feeding. The appendages bears long, slender and equally spaced ventral spines furnished with dense rows of long and fine auxiliary spines. This suggests that it was a microphagous suspension feeder, using its appendages for sweep-net capture of food items down to 0.5 mm, within the size range of mesozooplankton such as copepods. *Tamisiocaris* demonstrates that large, nektonic suspension feeders first evolved during the Cambrian Explosion, as part of the adaptive radiation of anomalocarids. The presence of suspension-feeders in the early Cambrian, together with evidence for a diverse pelagic community containing phytoplankton[7,8] and mesozooplankton[7,9,10], indicates the existence of a complex pelagic ecosystem[11] supported by high primary productivity and nutrient flux[12,13]. Cambrian pelagic ecosystems appear to have been more modern than previously believed.

Tamisiocaris borealis, from the early Cambrian Sirius Passet fauna of North Greenland, has previously been described as a possible anomalocarid on the basis of a disarticulated frontal appendage[6]. New fossils not only substantiate the anomalocarid affinities of *Tamisiocaris*, but also suggest that it was adapted to prey microphagously on mesozooplankton.

Tamisiocaris borealis is now known from five isolated frontal appendages and two appendages associated with a head shield. Frontal appendages (Fig. 1)

measure ≥ 120 mm in length, comparable in size to the later *Anomalocaris canadensis*[14], whereas the total size of the body is not known. As in other anomalocarids, the appendage consists of discrete, sclerotized articles. All specimens are preserved with the ventral spines parallel to the bedding plane, and the articles show no evidence of distortion due to compaction. It is therefore assumed that the articles were transversely compressed, with an oval cross section in life. The appendage consists of at least 18 articles, versus 14 in, for example, *A*. *canadensis*. Articles are separated by triangular arthrodial membranes (Extended Data Fig. 2b,c). These extend almost to the dorsal margin of the appendage; ventrally, the membrane is 33-50% the length of the articles, suggesting a well-developed flexural ability.

The appendage curves downward distally, with the strongest curvature around the second and third article. The first article is straight, and longer than the next three combined. It bears a single pair of ventral spines near its distal margin, which are stout and angled backwards (Fig. 1a) as in *Anomalocaris briggsi*[5]. The next 17 articles each bear pairs of long and delicate ventral spines inserted at the mid-length of the article. These are evenly spaced along the appendage about 5-6 mm apart. The spines diverge ventrally such that each pair forms an inverted V-shape. Unlike *A. canadensis*, in which longer and shorter spines alternate and taper distally, the ventral spines are all of similar length, measuring 26-27.5 mm along the full length of the appendage (Fig. 1a,b, Extended Data Fig. 1-3). A similar condition is seen in *A*. *briggsi*. The ventral spines curve posteriorly, again as in *A*. *briggsi*, but unlike any other anomalocarids. Individual spines appear flattened, with a median rod and thinner lamellar margins (Extended Data Fig. 1c). In addition, ventral spines are

frequently kinked, and sometimes broken, suggesting that they were weakly sclerotized and flexible.

As in many other anomalocarids[5,15], the anterior and posterior margins of the ventral spines bear auxiliary spines (Fig. 1c, Extended Data Fig. 1c, 2d, 3), but they are unusually long in *Tamisiocaris* —measuring 4.2-5.0 mm in length— and extremely slender. Auxiliary spines form a comblike array, being spaced 0.3-.85 mm apart, with a median spacing of 0.49 mm. The length and spacing are such that adjacent spine combs between spines would overlap or interdigitate.

One specimen consists of two associated appendages in subparallel orientation (Extended Data Fig. 4). Proximally, they join a large, elliptical head shield. The head shield is larger than in *Anomalocaris canadensis*, but is not enlarged to the same degree as seen in *Peytoia nathorsti* and *Hurdia victoria*. Eyes are not preserved.

The affinities of *Tamisiocaris* were examined in a cladistic analysis to explore its position within the anomalocarids. The analysis recovers a clade consisting of *Tamisiocaris borealis* and *Anomalocaris briggsi* (Fig. 3). This clade, which we name the Cetiocaridae (cetus: whale, shark or other large marine animal; and caris: sea crab), is diagnosed by long, slender, and recurved ventral spines, and the presence of numerous auxiliary spines. *Tamisiocaris* is more specialized, however, in having flexible ventral spines and densely packed auxiliary spines. The cetiocarids are a sister to Hurdiidae, a clade containing *Hurdia victoria, Peytoia nathorsti*, and related species. Outside these taxa lies a clade of plesiomorphic forms including *Anomalocaris canadensis, A. saron*, *Amplectobelua* spp., and relatives.

The hypothesis that *Tamisiocaris borealis* engaged in suspension feeding

can be evaluated by comparisons with extant analogues (Extended Data Figure 5). Suspension feeding crustaceans, such a cirripedes (barnacles), atyid shrimp, copepods, cladocerans, mysids and euphausiaceans (krill) share a suite of adaptations for sieving particles out of the water column that are also found in the Cetiocaridae (Extended Data Figure 5). These include appendages with (i) very elongate, flexible setae and/or setules and (ii) regular spacing, and (iii) close spacing of setae/setules. These features create a net with a regular mesh size that efficiently traps all particles above a threshold set by the setal spacing. The feeding limbs sieve particles out of the water, concentrate them by contraction, and carry them to the mouth[16]. The suspension feeding apparatuses of vertebrates have a similar morphology. Suspension-feeding teleosts and some sharks use a mesh formed by long, slender, and closely spaced gill rakers. The feeding apparatus of mysticete whales consists of arrays of baleen plates that wear into elongate fringes[17].

The mesh size of the capture apparatus is closely related to prey size: Right whales specialise on small copepods (fringe diameter 0.2 mm) while blue whales (fringe diameter 1 mm) feed on larger krill[18]. A survey of diverse suspension feeders, from cladocerans to blue whales, shows a linear relationship between mesh size and minimum prey size (Fig. 4). While larger prey can be captured, the bulk of the prey is close to the mesh size of the suspension apparatus.

Based on the morphologies seen in modern animals, a suspension-feeding anomalocarid would be predicted to have evolved a setal mesh, with large appendages bearing long, flexible setae to increase capture area, with close, regular setal spacing. This is indeed the morphology observed in *Tamisiocaris*.

Furthermore, one can use the mesh dimensions to predict the size of the prey caught by *Tamisiocaris*. Spacing of the auxiliary spines in *T. borealis* suggests that it could suspension food items from the water column down to 0.5 mm, while linear regression from extant suspension feeders (Fig. 4) predicts a slightly larger minimum particle size of 0.71 mm. Known mesozooplankton, from small carbonaceous fossil assemblages from the Cambrian Series 2[9,10], include isolated feeding appendages from crustaceans, including putative copepods. Based on comparisons with mandibles of modern counterparts[10] the largest known specimens reached diameters of 1.5 to 2.7 mm. We hypothesise that feeding was accomplished by alternate sweeping of the appendages, with entrapped prey being sucked[19] up by the oral cone (Supplementary information animation 1 and 2).

In the context of the phylogenetic analysis presented here (Fig. 3), different anomalocarid clades evolved distinct frontal appendage morphologies and feeding strategies. Primitive forms such as *Anomalocaris canadensis* had raptorial appendages with stout, trident-like spines, well-suited to impaling large, free-swimming or epifaunal prey[3] (Extended Data Fig. 6a,b). *Amplectobelua* had pincer-like appendages[20] (Extended Data Fig. 6c,d) that would have been effective in seizing and tearing apart relatively large, slow-moving animals. In hurdiids, the appendages bear opposing pairs of spines, which may have functioned as jaws or in sediment sifting[15] (Extended Data Fig. 6e,f). Finally, cetiocarid frontal appendages are specialized as sweep nets (Extended Data Fig. 6g,h). This extraordinary range of appendage morphologies shows that, far from being a failed experiment, anomalocarids staged a major adaptive radiation during the Cambrian Explosion, evolving to fill a range of niches as nektonic

predators, much like the later radiations of vertebrates[21] and cephalopods[22] by also becoming secondary suspension feeders.

The existence of suspension feeding in anomalocarids also has implications for the structure of early Cambrian pelagic food webs (Extended Data Fig. 7). It had been assumed that a diverse planktonic fauna and suspension feeding animals did not evolve until the late Cambrian[23] and thus the complexity of the pelagic food web evolved in a delayed, piecemeal fashion. However, the discovery of large suspension feeders in the early Cambrian suggests a well-developed pelagic biota supported by high primary productivity and abundant mesozooplankton, because large animals can only exploit small prey when they exist at high densities. Whales, whale sharks and basking sharks exploit highly productive areas such as upwelling zones and seasonal plankton blooms at high latitudes[24]. This general observation holds for all microphagous suspension feeders ranging from cladocerans, to anchovies, to red salmon, to blue whales: a high density of food particles is required to sustain an actively swimming suspension feeder.

Other evidence for high primary productivity in the Cambrian includes vast deposits of phosphorites and increased terrestrial nutrient flux[12,13,25], imply that high productivity may have been a global phenomenon in the Cambrian. Furthermore, the Cambrian also witnessed a radiation of spiny acritarchs, which are thought to have lived as microscopic phytoplankton, replacing larger Neoproterozoic benthic forms[7,8]. Complex minute crustacean feeding appendages also occur in lower and middle-upper Cambrian rocks[9,10], demonstrating the presence of diverse mesozooplankton, preying on phytoplankton. Abundant vetulicolians in Sirius Passet[26] (with hundreds of

specimens collected on recent expeditions) may also have been suspension feeding upon phytoplankton (Extended Data Fig. 6). One tier up, *Tamisiocaris* would have preyed upon the mesozooplankton as would the common nektonic arthropod *Isoxys volucris*[27]. Other pelagic predators known from *Lagerstätten* elsewhere would also have fed on mesozooplankton, including ctenophores, cnidarians, chaetognaths[11] and pelagic arthropods[28] (Extended Data Fig. 7). The Cambrian pelagic food web was therefore highly complex[28,29], containing multiple trophic levels, including pelagic predators[11] and multiple tiers of suspension-feeders. This underscores the remarkable speed with which a modern food chain was assembled during the Cambrian Explosion.

Finally, the discovery of a suspension feeding anomalocarid has implications for debates concerning the predictability of evolution, or lack thereof. One view holds that evolution is ultimately unpredictable[30]. The striking convergence between *Tamisiocaris* and extant suspension feeders, however, suggests that while different groups occupy ecological niches at different times, the number of viable niches and viable strategies for exploiting them are limited. Furthermore, the derivation of the suspension-feeding *Tamisiocaris* from a large apex predator parallels the evolution of suspension feeding pachycormid fish[1,21], sharks and whales[2]. In each case, suspension feeders evolved from nektonic macropredators. This suggests that evolution is canalized not only in terms of outcomes, but in terms of trajectories. The result is that independent evolutionary experiments by animals as different as anomalocarids, fish and whales have converged on broadly similar outcomes.

METHODS SUMMARY

Specimens were collected in the field and photographed in the lab, coated or uncoated and submerged in water. A digital reconstruction of the *Tamisiocaris* feeding appendage were made in order to infer the range of motions. The suspension mesh diameter and prey width were collected from literature on extant suspension feeders to depict the linear relationship between these (see supplementary Methods). A cladistic analysis containing 31 taxa and 51 characters was collated and analysed in PAUP* 4.0 b10 and TNT (see Supplementary Information).

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Author information. Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to J.V. (jakob.vinther@bristol.ac.uk).

Figure 1 | *Tamisiocaris borealis* Daley and Peel, 2010 frontal appendages from Sirius Passet, Lower Cambrian, North Greenland. a, Isolated and relatively complete appendage, MGUH 30500 (Geological Museum at the University of Copenhagen). **b**. Isolated appendage, preserving auxiliary spines in great detail, MGUH 30501. **c**, detail of spine in **b**. All specimens photographed submerged in water with high angle illumination.

Figure 2 | A digital reconstruction of *Tamisiocaris*. a. Single appendage indicating the articulating membranes (Am), articles (Art), spines (Sp) and auxiliary spines (As). **b**. Possible sequence of movement of the frontal

appendage of *Tamisiocaris*. See also Supplemental Information Videos 1 and 2.

Figure 3 | Phylogeny of anomalocarids. Strict consensus of 91 trees derived from an analysis of 31 taxa and 54 characters using parsimony in PAUP* 4.0b10. *Tamisiocaris borealis* forms a clade with *Anomalocaris briggsi*, here named Cetiocaridae.

Figure 4 | Diagram depicting the relationship between suspension mesh size and the food items consumed by suspension feeders. *Tamisiocaris* is indicated by the dotted line based on a mesh width of 0.51 mm. The diagram is collated from a range of modern suspension feeders, see Online Methods section.

Methods section

Material. Five specimens of *Tamisiocaris borealis (*MGUH 30500-30504*)* were collected in situ from the main exposure (Locality 1) (Fig. 1, Extended Data Figure 1-3) of Sirius Passet[1,2,3], Nansen Land, North Greenland during expeditions in 2009 and 2011. The type specimen, described by Daley and Peel (MGUH 29154)[3], was collected on an earlier expedition.

Photography. Specimens were photographed, using a Nikon d800, with a Nikon micro Nikkor 105 mm F/2.8G AF-S VR and Nikon AF micro Nikkor 60 mm F/2.8D lens in low angle light using an LED light source after coating with MgO smoke. Specimens were also photographed submerged in water with high angle polarized lighting in order to maximize reflectivity of the specimen. Images were cropped and image contrast and colour levels were adjusted in Adobe Photoshop CS6.

Digital reconstruction. Proportions of articles, spine length, and the extent of arthrodial membrane in the reconstruction are based on a single schematic line

drawing created from interpretative drawings of the specimens. This was used as a blueprint to model a subdivision surface mesh in Cheetah3D 6.2.1. The reconstruction was rigged with an armature of 19 bones, using forward kinematics. The bones were laid along the main axis of the articles in the dorsal quarter of the articles, where the pivot joints must have been placed judging from the extent of the arthrodial membrane (Extended Data Fig. 2). The mesh was bound to the armature with full vertex weight assigned to the articles, less than half vertex weight to the adjacent arthrodial membrane area. This ensured rigid behavior of the articles upon rotation. For the animation sequence, bones were rotated to the maximum extension (Fig. 2, Supplemental Information Video 1 and 2) permitted by the arthrodial membrane areas (Extended Data Fig. 2).

***Comparisons with modern suspension feeders*.** Published records of the mesh size and width of the diet in various suspension feeders were collated and plotted in a double logarithmic diagram in order to investigate their possible correlation. Included taxa included, cladocerans: *Chydorus spaericus*[4], *Daphnia hyalina*[4], *D. magna*[4], *D. galeata*[4]; Mysids: *Mesodopsis woolridgei*[5], *Rhopalophtalmus terranatalis*[5]; Krill: *Euphausia superba* (references); Japanese anchovy, *Engraulis japonicus*[6]; Pacific Round Herring, *Etrumeus teres*[6], Rainbow trout, *Oncorhyncus mykiss*[7]; Greater flamingo, *Phoenicopterus antiquorum*[8]; Lesser flamingo, *Phoenicomaia minor*[8]; Whale Shark, *Rhincodon typus*[9]; Mysticete whales: Right Whale[10], Blue Whale[10], Bowhead whale[11]. For baleen whales, the effective mesh size of the baleen plates is contingent on the speed of water movement across the baleen plate. In bow head whales, speeds of 5 km/h while feeding is reported, thus the fastest measured speed of 100 cm/s measured across multiple baleen plates was used as effective mesh diameter

(inter fringe diameter) while for right whale and blue whale the diameter of the baleen fringe was used as a proxy for filter mesh size.

We did a linear ($y = 1.6675x$; $R^2 = 0.26843$) and power (Lower bound: $y = 1.4452x^{1.0083}$; $R^2 = 0.91627$, Upper bound: $y = 11.772x0.8928$

RÇ = 0.8708) regression, which are similar in trajectory.

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Extended Data Figure 1 | *Tamisiocaris borealis* MGUH 30500, frontal appendage. a. Part photographed in low angle lighting coated with MgO. **b**. Camera lucida drawing with indications of spines (s1-s15); spines, broken at the base (Bs). **c**. Detail of spine preserving auxiliary spines in relief (arrowed).

Extended Data Figure 2 | *Tamisiocaris borealis* MGUH 30500, frontal appendage. a. Part, photographed submerged in water and with high angle illumination. **b**. Counterpart, displaying articulating membranes across the appendage indicated by their relatively lower reflectivity. **c**. Detail of **b**, and the articulating membranes (Am) and articles (Art) along the mid section of the appendage. d. Detail of broken spine in **b**, displaying auxiliary spines.

Extended Data Figure 3 | *Tamisiocaris borealis* MGUH 30501 frontal appendage with well preserved auxiliary spines. a. Part. **b**. Detail of auxiliary spines in **a**. **c**. Schematic drawing of MGUH 30501, from a combination of part and counterpart. **d**. Counterpart. **e**. Detail of **d** showing regular arrangement of auxiliary spines.

Extended Data Figure 4 | MGUH 30502 frontal appendages and head shield assemblage, lateral view. a. Part. **b**. Camera lucida drawing of the part indicating the head shield (Hs), left frontal appendage (Lfa) and right frontal appendage (Rfa). Partially superimposed on the specimen is the other arthropod *Buenaspis* (Ba). **c**. Detail of distal section of frontal appendages in counterpart. **d**. detail of head shield.

Extended Data Figure 5 | Modern crustacean suspension feeders. a. The Northern krill, *Meganyctiphanes norvegica* (Image credit: Wikipedia/Øystein Paulsen). Insert: reconstruction of the thoracic region of the krill, *Euphausia suberba*, from Barkley (1940). **b**. Proximal elements of the thoracopods in *E. suberba* (Image credit, Uwe Kils). **c**. Distal elements of the thoracopods in *E.*

suberba (Image credit, Uwe Kils). **d**. The filter basket in an undetermined mysid (Image credit Wikipedia/Uwe Kils). **e**. Thoracopod from the cirripede *Darwiniella angularis* Chen, Lin and Chan 2012, with permission from the authors.

Extended Data Figure 6 | Schematic drawings of different anomalocarid frontal appendages. a. *Tamisiocaris borealis*, **b**. *Anomalocaris briggsi*, **c**. *Anomalocaris canadensis*, **d**. *A.* cf. *saron*, NIGP 154565, **e**. *Amplectobelua symbrachiata*, **f**. *Amplectobelua stephenensis*, **g**. *Hurdia victoria*, **h**. *Stanleycaris hirpex*.

Extended Data Figure 7 | A schematic overview of some of the known components the early Cambrian pelagic food web. At the base of the food chain was phytoplankton in the form of acritarchs and most likely other forms with no apparent fossil record. Diverse mesozooplankton were present as copepod and branchiopod-like crustaceans feeding on phytoplankton, along with vetulicolians, which exhibit a morphology suggesting suspension feeding similar to basal chordates. Larger pelagic predators such as chaetognaths, larger arthropods and potentially also ctenophores preyed upon the mesozooplankton. *Tamisiocaris* would similarly have fed on the mesozooplankton. The presence of a large nektonic suspension feeder suggests a high abundance of primary producers and mesozooplankton. Other anomalocarids, such as *Anomalocaris* and *Amplectobelua* were present as some of the macrophagous apex predators at this time.